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Title: Eco-engineering urban infrastructure for marine and coastal biodiversity: which interventions have the greatest ecological benefit?

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40

41 **Running title:** Eco-engineering marine urban infrastructure

42

43 **Abstract**

44 1. Along urbanised coastlines, urban infrastructure is increasingly becoming the dominant
45 habitat. These structures are often poor surrogates for natural habitats, and a diversity of eco-
46 engineering approaches have been trialled to enhance their biodiversity, with varying success.

47 2. We undertook a quantitative meta-analysis and qualitative review of 109 studies to
48 compare the efficacy of common eco-engineering approaches (e.g. increasing texture,
49 crevices, pits, holes, elevations and habitat-forming taxa) in enhancing the biodiversity of key
50 functional groups of organisms, across a variety of habitat settings and spatial scales.

51 3. All interventions, with one exception, increased the abundance or number of species of one
52 or more of the functional groups considered. Nevertheless, the magnitude of effect varied
53 markedly among groups and habitat settings. In the intertidal, interventions that provided
54 moisture and shade had the greatest effect on the richness of sessile and mobile organisms,
55 while water-retaining features had the greatest effect on the richness of fish. In contrast, in
56 the subtidal, small-scale depressions which provide refuge to new recruits from predators and
57 other environmental stressors such as waves, had higher abundances of sessile organisms
58 while elevated structures had higher numbers and abundances of fish. The taxa that
59 responded most positively to eco-engineering in the intertidal were those whose body size
60 most closely matched the dimensions of the resulting intervention.

61 4. *Synthesis and applications*: The efficacy of eco-engineering interventions varies among
62 habitat settings and functional groups. This indicates the importance of developing site-
63 specific approaches that match the target taxa and dominant stressors. Furthermore, because
64 different types of intervention are effective at enhancing different groups of organisms,
65 ideally a range of approaches should be applied simultaneously to maximise niche diversity.

66
67 **Keywords:** eco-engineering interventions, artificial structure, crevice, depression, habitat-
68 forming species, microhabitat, protrusion, rockpool, seeding, urban infrastructure

69 **Introduction**

70
71 Of the many human activities presently contributing to habitat loss and species extinctions,
72 urbanisation is generally considered to have one of the greatest impacts across local to
73 regional scales (Lotze *et al.* 2006; Grimm *et al.* 2008). Over 50% of the human population
74 now lives in urbanised areas (United Nations Population Fund 2007), with areas within 100
75 km of the coastline particularly heavily developed, housing over 40% of the global
76 population and 60% of its largest cities (>5 million inhabitants, Firth *et al.* 2016a). The urban
77 ecological footprint extends beyond city boundaries and increasingly sprawls into marine and
78 coastal waters (Duarte *et al.* 2008). In addition to introducing pollutants, such as heavy
79 metals, nutrients, artificial light and sound, to marine and coastal habitats (Daoji & Daler
80 2004; Halpern *et al.* 2008), urban environments introduce infrastructure (Dafforn *et al.* 2015).
81 This infrastructure is used for a range of purposes including coastal protection (e.g. seawalls,
82 breakwaters, groynes), boating or recreational activities (e.g. marinas, piers, pontoons),
83 supply of energy or resources (e.g. oil, gas platforms) and enhancement of fisheries yield
84 (e.g. artificial reefs).

85
86 Urban infrastructure impacts on natural ecosystems in a variety of ways, including habitat
87 loss and fragmentation, as well as modification of ecological connectivity, ecosystem
88 functioning and services, and the physico-chemical environment (Fischer & Lindenmayer
89 2007; McKinney 2008; LaPoint *et al.* 2015; Bishop *et al.* 2017). The net effect is urbanised
90 ecosystems that are fundamentally different in structure and function to the natural habitat
91 which they displace (Airoldi *et al.* 2015; Gittman *et al.* 2016; Heery *et al.* 2017). In some
92 instances the need for urban infrastructure may be circumvented by adding or restoring
93 natural habitats that enhance biodiversity and provide essential functions (Sutton-Grier,
94 Wowk & Bamford 2015; Dethier, Toft & Shipman 2016). For example, the conservation,

95 restoration and/or establishment of coastal plants, and shellfish and coral reefs that dissipate
96 wave energy and stabilise shorelines may prevent the need for revetments and seawalls
97 (Arkema *et al.* 2013) and also enhance fisheries productivity and sequestration of carbon
98 (Barbier *et al.* 2011). In heavily modified environments, conservation and restoration of
99 natural habitats may, however, not be feasible, and novel solutions are required (Hobbs,
100 Higgs & Harris 2009; Lundholm & Richardson 2010). Amongst these, eco-engineering – the
101 inclusion of ecological principles in the design of infrastructure to enhance its ecological
102 value (Bergen, Bolton & Fridley 2001) – can benefit terrestrial and marine environments
103 alike (Chapman & Underwood 2011; Francis & Lorimer 2011). Ideally, ecological values
104 should be incorporated in infrastructure during the design phase to have greatest effect, but
105 existing structures may also be modified to promote species of conservation, commercial or
106 functional interest and to enhance native biodiversity (Chapman & Blockley 2009; Dugan *et*
107 *al.* 2011).

108

109 In terrestrial environments, green walls and roofs have been designed to enhance biodiversity,
110 restore connectivity to certain faunal groups, and bolster desired ecosystem functions
111 (Lundholm & Richardson 2010; Francis & Lorimer 2011; Braaker *et al.* 2014). Analogous
112 approaches can be applied to the design of urban infrastructure in marine environments
113 (Chapman & Underwood 2011; Firth *et al.* 2014a). As compared to the largely horizontal and
114 topographically complex surfaces of natural substrates, marine urban infrastructure typically
115 has vertical, smooth, surface that reduces the area for attachment and the diversity of habitat
116 niches for organisms, and provides fewer refuges from predators, competitors and/or
117 environmental stressors (Bulleri & Chapman 2010; Loke & Todd 2016). Consequently, one
118 of the commonly utilised techniques for eco-engineering marine infrastructure has been to
119 increase surface area and/or habitat complexity of the hard substrate at a range of scales (mm
120 to metres) using either additive (i.e. attachment of protruding structures) or subtractive (i.e.
121 drilling, removal of substrate) processes (Chapman & Underwood 2011). Additive
122 approaches have utilised both abiotic substrate, and ‘seeding’ with habitat-forming taxa such
123 as barnacles, bivalves, canopy-forming algae, branching coralline algae or corals (e.g.
124 Dafforn, Glasby & Johnston 2012; Perkol-Finkel *et al.* 2012; Wilkie, Bishop & O'Connor
125 2012; Ferse *et al.* 2013). In the marine environment, the majority of eco-engineering to date
126 has been small-scale experimental additions of habitat features to existing urban
127 infrastructures (Chapman & Underwood 2011), with relatively few attempts to incorporate
128 features into new urban infrastructures (but see Chapman & Blockley 2009, Firth *et al.* 2013

129 for some exceptions). These interventions have had varying degrees of success in enhancing
130 native biodiversity, and in some instances may serve as ecological traps if they lead to
131 organisms utilising habitats that reduce their fitness (Hale, Treml & Swearer 2015; Hale,
132 Morrongiello & Swearer 2016). Despite this, quantitative studies of the factors that influence
133 the efficacy of such interventions in enhancing biodiversity are lacking.

134
135 The efficacy of eco-engineering interventions for enhancing the biodiversity of urban
136 infrastructures is likely to vary across species and environments as well as the spatial and
137 temporal scales of the intervention. The stress gradient hypothesis predicts that positive
138 associations will be greatest in environments where biotic or abiotic stressors are greatest,
139 and weakest in environmentally benign environments (Bertness & Callaway 1994). Hence,
140 interventions that ameliorate abiotic stressors such as temperature and desiccation may be
141 expected to have increasingly strong influences across the intertidal gradient (Bateman &
142 Bishop 2017). Interventions that weaken biotic interactions may be most effective in
143 environments with high predator abundances, or in which competition is intense (Chapman &
144 Underwood 2011; Strain *et al.* in review). Additionally, because responses of organisms to
145 complexity are dependent on body size (Hacker & Steneck 1990; McAbendroth *et al.* 2005),
146 an organism may benefit most from an intervention that adds microhabitats that are a similar
147 order of magnitude to its size (Köhler, Hansen & Wahl 1999). The effects of the interventions
148 can also vary through time depending on the recruitment and growth of the organisms, the
149 mobility of the organism and the successional stage of the community (Firth *et al.* 2016a).
150 For example, the effectiveness of some interventions may only become apparent after
151 sufficient time has elapsed for colonisation to occur (Evans 2016). Alternatively, the efficacy
152 of others may plateau over time, where seeding of structures with biogenic habitats speeds up
153 succession but does not change the endpoint after a number of years (Ferse *et al.* 2013).
154 Studies quantifying how the efficacy of these interventions varies across multiple locations,
155 environments, spatial-scales and time points are lacking.

156
157 In this study, we used a meta-analysis and a qualitative literature review to assess sources of
158 variation in the efficacy of interventions aimed at enhancing the biodiversity of both new and
159 existing marine urban infrastructure through the creation of novel microhabitats. We expected
160 that across all scales (ranging from mms to 10s of meters), the addition of complex
161 microhabitats (i.e. texture, crevices, pits, water retaining, holes, small elevations, large

162 elevations, seeding) to urban infrastructure would produce an overall positive effect on the
163 number and abundances of species for specific functional groups (sessile, mobile, benthic,
164 fish) and habitat-forming taxa (barnacles, bivalves, branching coralline, canopy algae, coral).
165 Nevertheless, we expected that the magnitude and direction (positive or negative) of effects
166 of interventions on the abundance and richness of taxa would vary between habitat contexts
167 (intertidal and subtidal) across which the identity of dominant stressors varies, through time,
168 between interventions applied to new and existing infrastructure and among functional
169 groups of organisms, reflecting variation in their niche requirements, and body size.

170

171 **Materials and methods**

172 *Literature search*

173 We searched the literature using Google Scholar and Web of Science for manipulative and
174 mensurative field studies in intertidal and subtidal estuarine and coastal marine systems that
175 examined the ecological effects of adding microhabitats to urban infrastructure (i.e. directly
176 to structures or to settlement panels) either during construction or by retrofitting. The search
177 terms included ('microhabitats*: texture*, roughness* crevices*, cuts*, fissures*, grooves*,
178 pits*, rockpools*, tidal pools*, rock pools* flowerpots* holes*, ridges*, elevations*, towers*,
179 raises*, relief*, mimic*, rope*, ribbons*, brushes*') and ('seeding*, transplants*, planting*,
180 epoxy*, glue*, habitat-forming*, barnacles*, bivalves*, mussels*, oysters*, canopy*, kelps*,
181 coral*, branching coralline*, corticated turf*, branching turf*') on ('artificial habitat*,
182 artificial reefs*, artificial structure*, tiles* or settlement plates*'). We also searched the
183 reference and citation lists of each article identified using the same search terms.

184

185 We selected studies for the analyses that compared between otherwise similar urban
186 infrastructure with and without the intervention: (1) the number of species per unit area (i.e.
187 species density); (2) the abundance of all species within one or more functional groups:
188 sessile algae and invertebrates (hereafter 'sessile'), mobile invertebrates (hereafter 'mobile'),
189 all sessile algae and sessile and mobile invertebrates combined (hereafter 'benthic') and fish
190 (hereafter 'fish'); and/or (3) the species density and total abundance of key habitat-forming
191 taxa (see Table 1 examples). For each study, the nature of the intervention was classified
192 according to whether it added texture, crevices, pits, intertidal water retaining features,
193 subtidal holes, elevations, or habitat-forming species (see Table 1 for definitions) to urban
194 infrastructure. For studies that tested the effects of multiple types of intervention or single

195 types of intervention, across multiple sites each intervention and site was used as a replicate
196 for the analyses (see below for further details).

197

198 *Data extraction*

199 We found 388 studies through the literature search, from which 109 were suitable for
200 inclusion in our meta-analysis (Table S1) after exclusions (i.e. lack of controls, data on single
201 species or a subset of species from a functional group, confounding with other factors,
202 relevant data not presented either in text or graphs). A list of the studies used is provided in
203 the Data sources section. For each study, we recorded the sample size, and the mean and
204 standard deviation (when reported) of the number and/or abundance of each functional group
205 on urban infrastructure receiving the intervention and on otherwise similar unmanipulated
206 substrate (control). In instances where data were presented in the figures, we used GetData
207 Graph Digitizer version 2.25.0.32 (www.getdata-graph-digitizer.com) to extract means and
208 standard deviations. We also recorded the geographical location of each study, the time
209 interval after which the invention was fitted or built (in months; hereafter ‘time’), the type of
210 intervention either retrofitted or built (hereafter ‘method’), the area across which the
211 intervention was applied (m²) and the dimensions of the unit of intervention (i.e. depth of
212 crevices, pits, holes, intertidal water retaining features and height of elevations and habitat-
213 forming taxa), where available.

214

215 *Data analysis*

216 For studies reporting means, standard deviations and sample sizes (or from which these data
217 could be extracted from figures), we calculated the effect size of the various interventions on
218 variables of interest (i.e. abundance and number of species) as Hedge’s g standard mean
219 difference (SMD) (Hedges 1981). We chose the SMD effect size in the meta-analysis rather
220 than the log ratio because these data contained many zeros (i.e. no species observed and/or no
221 variance observed between replicates within the same treatment), (Borenstein *et al.* 2010).
222 For the analysis, the effects of interventions were tested against the control using a random
223 effects model as there was significant heterogeneity between studies (determined by
224 measuring heterogeneity via Cochran’s Q, and testing it against a χ^2 distribution with n-1
225 degrees of freedom, where n is the number of studies). The model was fitted using the
226 Hedges random effects estimator (Hedges 1981).

227

228 For studies that tested the effect of interventions at different sites, we treated each site as a
229 separate study in the meta-analysis. We tested for links between these by adding study
230 identity as a moderator in the model. When sites from the same study were linked, the results
231 were adjusted by adding study identity as a moderator in a multilevel random effects model.

232
233 For each functional group and habitat-forming taxa we assessed how the magnitude and
234 direction (positive or negative) of effects varied with the size of the intervention area (m^2), the
235 depth or height of the unit of intervention (either the depression or elevation in mm to m), the
236 time after implementation of the intervention that monitoring was done (months), method
237 (retrofitted or built) and differences between zones (intertidal or subtidal) and the type (Table
238 1) by adding these terms separately, as moderators in the models. Similarly, for each type of
239 intervention, we assessed how the magnitude and direction of effects varied across the
240 functional groups or habitat-forming taxa by including intervention type (Table 1) as
241 moderators in the models. For the water retaining features, only data on the species number
242 was presented in the studies, and not the species abundances. Therefore, we could not
243 compare the effects of water retaining features on species abundances to the other
244 interventions (i.e. texture, crevices, pits, small elevations, or seeding) in the analyses.

245
246 For studies that did not present the variance between replicates, we substituted in the
247 maximum standard deviation from studies on the same intervention (Furukawa *et al.* 2006;
248 Strain *et al.* 2014). There were no detectable differences in effect sizes between the studies
249 with and without standard deviations (based on overlapping 95% confidence intervals). We
250 also tested and found no differences in the effects of the microhabitats between the
251 manipulative (97%) or mensurative (3%) studies (data not shown).

252
253 We checked whether there was a significant correlation between the effect size and sample
254 size, as a measure of publication bias using qualitative tests (weighted frequency histogram,
255 funnel plots and Q-Q normality plots of effect sizes). We also assessed the number of studies
256 required to increase the p-value to above 0.05, using the Rosenthal's fail-safe number test
257 (Tables S2-3). All analyses and plots were undertaken using the R package, *metafor*
258 (Viechtbauer 2010) in R gui 3.1.1 (R Core Team 2016).

259
260 In addition, we undertook a qualitative review that included studies that did not present data
261 that could be extracted for the analysis (i.e. only written statements about their results). For

262 each type of intervention, we calculated the proportion of studies reporting significant versus
263 non-significant results. We tested for differences in the proportion of significant studies
264 between intertidal and subtidal zones, or among functional groups or habitat-forming taxa
265 using χ^2 proportions tests.

266
267 For both the overall meta-analysis and qualitative review, we used the data from the final
268 sampling period of each study. We only performed analyses on interventions with three or
269 more studies (Tables S2-6).

270

271 **Results**

272 Of the 109 studies from which data were extracted, 23% focused on texture and 21% on
273 crevices. The remaining studies, focused on pits, water retaining features, subtidal holes,
274 small elevations, large elevations and seeding, each contributed between 3-12% to the total
275 number of studies used in the review. 67% of studies described interventions that were
276 retrofitted to existing structures, with the remainder describing interventions that were
277 incorporated at the design stage (Table S1). Of the studies describing interventions at the
278 design stage, 72% were on artificial reefs (Table S1). The studies were not evenly distributed
279 around the globe (Fig. 1) and much (60%) of the research was conducted in Australia
280 (Sydney), Israel (Red Sea), Europe (various locations) and North America (east coast).

281

282 The studies were published between 1946 and 2016, with a sharp increase in number through
283 time, mainly between 1990 and 2016 (Fig. 2). This trend is likely to be driven in part by the
284 increasing urbanisation of marine coastlines across the globe and the strong associated
285 interest in eco-engineering approaches. Each intervention type had studies from multiple
286 laboratories, years and countries, indicating the review conclusions are not strongly biased
287 towards an individual country or time point (Table S1).

288

289 Most types of intervention (all but the addition of large elevations) significantly enhanced the
290 number and/or abundance of species for at least one key functional group and/or habitat-
291 forming taxon relative to the control (Figs. 3, 4, 5; Tables S2-S6). Interestingly, in only one
292 instance - the addition of texture to the subtidal – was the abundance of a group (the
293 barnacles) significantly reduced relative to the control (Figs. 3-5). The most effective
294 interventions in increasing the number of species were water retaining features (mean [\pm SE]
295 difference for sessile and benthic species = 5.0 ± 4.4) and intertidal pits (mean [\pm SE]

296 difference for benthic species = 4.7 ± 2.1) and to a lesser extent intertidal crevices (mean
297 [\pm SE] sessile species = 2.2 ± 1.6), and subtidal soft interventions (mean [\pm SE] difference in
298 fish species = 1.6 ± 2.0) and seeding (mean [\pm SE] difference in sessile and fish species = 2.4
299 ± 2.8). There were no detectable differences in effects of retrofitted or built interventions on
300 the number or abundances of species, so these methods were pooled for the final analyses
301 (Tables S2-S3).

302

303 For many of the interventions (texture, crevices, pits, subtidal holes, small elevations and
304 large elevations, soft structures and seeding), the area of the intervention had a weak non-
305 significant positive effect on the number of species (Table S2-S3). In contrast, for intertidal
306 water retaining features, there was a significant positive effect of intervention area on the
307 number of species for each of the functional groups (Table S2). There was no relationship
308 between area of intervention and abundances of species for any of the interventions (Tables
309 S2-S3). As predicted, the effect of most of the interventions (texture, crevices, pits) differed
310 between zones (Tables S2-S6). In contrast, there were no clear effects of the height or depth
311 of the unit of manipulation (i.e. depression or elevation), or the time (months) of the
312 intervention on the species number or abundance (Tables S2-S3).

313

314 Overall the results from the meta-analysis and the qualitative review showed similar trends
315 (Table 2). For each intervention we highlight the results of the meta-analysis where available
316 and the results from the qualitative review where there was insufficient information presented
317 to undertake the meta-analysis.

318

319 *Effect of intervention type on the number and abundances of species by functional group*

320 The efficacy of the interventions in enhancing the species number and abundance of key
321 functional groups varied among categories (Figs. 3, 4; Table S4-S6). For sessile organisms,
322 the meta-analysis demonstrated that crevices, water retaining features, or seeding in the
323 intertidal zone resulted in greater increases in the number of species than any of the other
324 interventions tested, in either the intertidal or subtidal zone ($Q_4 = 40.0$, $p < 0.001$, Fig. 3,
325 Table S2). In contrast, the cover of sessile species displayed a greater positive response to
326 intertidal seeding and the addition of subtidal texture than to the other interventions ($Q_3 = 8.3$,
327 $p = 0.049$, Fig. 4, Table S3). For the mobile species, the qualitative review found that a
328 greater proportion of studies displayed significant effects of intertidal crevices, pits or
329 subtidal holes on abundances ($\chi^2_3 = 10.4$, $p = 0.015$) but not numbers of species ($\chi^2_3 = 7.3$, p

330 > 0.05), relative to the other interventions (Figs. 3, 4; Tables S4-S5). For fish, the meta-
331 analysis suggested subtidal soft features and seeding were most important for enhancing both
332 the number ($Q_4 = 36.0$, $p < 0.001$) and abundances of species ($Q_4 = 15.6$, $p = 0.004$) relative to
333 the other interventions tested (Figs. 3, 4; Tables S2-S3). As expected, the qualitative analysis
334 also showed that in a greater proportion of studies, intertidal water retaining features
335 enhanced the number of fish species as compared to the other interventions assessed ($\chi^2_4 =$
336 12.7 , $p = 0.013$; Fig. 3; Table S4).

337

338 Across the different interventions, intertidal water retaining features and seeding (irrespective
339 of zone) were the only habitats that significantly enhanced the number of species for multiple
340 functional groups (Figs. 3, 4; Table S4). The meta-analysis demonstrated that intertidal water
341 retaining features significantly increased the number of sessile, benthic and fish species, but
342 not mobile species relative to controls ($Q_3 = 9.2$, $p = 0.036$, Fig. 3, Table S2). Seeding
343 resulted in a significantly higher number ($Q_4 = 13.4$, $p = 0.009$) and abundance ($Q_4 = 36.8$, p
344 < 0.001) of intertidal sessile species and subtidal fish but not intertidal mobile species or
345 subtidal sessile species (Figs. 3, 4; Tables S2-S3).

346

347 In contrast, the addition of texture, crevices, pits, subtidal holes or soft structures to urban
348 infrastructure only enhanced the species number or abundance of a single functional group
349 (Figs. 3, 4; Tables 1, S2). The meta-analysis showed the addition of subtidal texture only
350 significantly enhanced the cover of sessile species (Figs. 3, 4; Table S2). Intertidal crevices
351 increased the number of intertidal sessile species and pits increased the number of benthic
352 species, but the qualitative analyses suggested both of these interventions in many studies
353 also resulted in higher abundances of mobile species (Figs. 3, 4; Tables S2, S4). Subtidal
354 holes only significantly increased the abundances of mobile species (Figs. 3, 4; Tables 1, S3),
355 while the addition of soft habitats significantly increased the number and abundances of fish
356 species (Figs. 3, 4; Tables 1, S2-S3).

357

358 *Effect of intervention type on the number and abundance of habitat-forming taxa*

359 As predicted, many of the interventions significantly increased the abundance of habitat-
360 forming taxa (Fig. 5; Tables S3, S6). For barnacles ($Q_7 = 7.8$, $p = 0.049$) and bivalves ($Q_6 =$
361 8.8 , $p = 0.048$), the meta-analysis showed the addition of intertidal crevices and pits resulted
362 in higher cover and/or counts relative to the other interventions tested (Fig. 5; Tables S3). In
363 contrast, for corals, the addition of subtidal pits had the greatest benefits of all the

364 interventions considered ($Q_2 = 10.5$, $p = 0.006$; Fig. 5; Tables S3). The qualitative analysis
365 also showed in a greater proportion of studies the addition of texture resulted in increased
366 cover of branching coralline ($\chi^2_5 = 18.0$, $p = 0.003$; Fig. 5; Tables S6), while small elevations
367 lead to higher cover of canopy-forming algae ($\chi^2_5 = 18.0$, $p = 0.003$, Fig. 5; Table S6)
368 relative to the other interventions tested.

369
370 Overall, the addition of pits had the greatest benefits for multiple groups of habitat-forming
371 taxa (Fig. 5; Tables S3, S5). The meta-analysis showed intertidal pits significantly increased
372 the abundances of barnacles and bivalves ($Q_5 = 88.7$, $p < 0.001$, Fig. 5, Table S3). The
373 qualitative review suggested this intervention could also lead to higher cover of branching
374 coralline algae while subtidal pits significantly increased the cover or counts of barnacles,
375 branching coralline algae and corals (Fig. 5; Table S6). The addition of texture to the
376 intertidal resulted in significantly higher counts and cover of barnacles, branching coralline
377 and slightly more bivalves and in the subtidal increased cover of branching coralline algae,
378 but there were no detectable effects of this intervention on the other taxa ($Q_7 = 30.7$, $p < 0.001$;
379 Fig. 5; Table S3). Crevices had significantly higher counts of barnacles and cover of bivalves
380 when situated in the intertidal, but there were no detectable effects of this intervention on
381 other intertidal taxa or in the subtidal ($Q_5 = 25.0$, $p < 0.001$; Fig. 5; Table S3, S5). The
382 qualitative analysis showed that a greater proportion of studies demonstrated intertidal water
383 retaining features resulted in significantly higher numbers of species of branching coralline
384 and canopy-forming algae ($\chi^2_2 = 11.9$, $p = 0.008$; Fig. 5; Table S6), and small elevations
385 increased the cover of intertidal canopy-forming algae ($\chi^2_2 = 5.6$, $p = 0.049$; Fig. 5, Table S6)
386 relative to the other interventions. Interestingly, there were no clear benefits of seeding on the
387 abundances of new recruits of bivalves, coral or canopy-forming algae ($Q_3 = 2.4$, $p > 0.05$;
388 Fig. 5; Table S3).

389 390 **Discussion**

391 The effective use of eco-engineering as a tool for enhancing the habitat value of urban
392 infrastructure requires knowledge of when and where interventions have greatest influence.
393 Despite this, most eco-engineering studies in marine environments have focused on a single
394 type of microhabitat-enhancing intervention, at one or few sites (e.g. Chapman & Blockley
395 2009; Browne & Chapman 2014; Firth *et al.* 2014a). Studies in natural systems demonstrate
396 how the responses of species assemblages to microhabitats can vary across environmental
397 gradients (e.g. Firth *et al.* 2014b; McAfee, Cole & Bishop 2016) and among taxa (e.g.

398 Bateman & Bishop 2017). Our study provides the first cross-study, quantitative assessment of
399 how the effectiveness of different interventions applied to marine urban infrastructure varies
400 among groups of organisms and environmental settings. As predicted (see reviews by
401 Dafforn *et al.* 2015; Dyson & Yocom 2015; Firth *et al.* 2016a), overall microhabitat-
402 enhancing interventions had a positive effect on the abundance and number of species across
403 the studies. Nevertheless, the magnitude of their effects varied considerably, from zero to
404 highly positive according to the type of intervention, the target taxa, and tidal elevation.

405
406 In the intertidal, thermal and desiccation stresses have long been implicated in setting
407 distributional limits (e.g. Wolcott 1973; Harley 2003) and the persistence of organisms can be
408 contingent on the availability of microhabitat refugia from such stressors (Silliman *et al.*
409 2011; Firth *et al.* 2016b; McAfee, Cole & Bishop 2016). Perhaps not surprisingly then, the
410 intertidal interventions with the largest influence on sessile organisms, including barnacles,
411 bivalves, branching coralline and canopy-forming algae, and on mobile organisms, were
412 crevices, pits, and water retaining features, each of which provide shading and moisture
413 retention at low tide (Fig. 6, Table 5, Garrity 1984; Underwood & Jernakoff 1984). Similarly,
414 fish, which in the absence of water retaining features cannot persist in the intertidal zone at
415 low tide, were strongly influenced by water-retaining interventions. In contrast, the addition
416 of small elevations had little, if any, effect on intertidal organisms, despite their capacity to
417 enhance surface area for attachment. In the intertidal, the groups of organisms that responded
418 most strongly to a particular type of intervention were those whose body size most closely
419 matched the dimensions of the unit of intervention (Fig. 6, Hacker & Steneck 1990;
420 McAbendroth *et al.* 2005). For example, small-scale enhancements, such as adding texture,
421 pits and crevices, were most effective for smaller bodied organisms such as barnacles and
422 bivalves. In contrast, larger interventions such as rock pools could also support larger species
423 such as branching coralline, canopy-forming algae and fish (Fig. 6).

424
425 Similarly, subtidal interventions that added depressions, as opposed to elevations, generally
426 had greatest positive effects on the majority of taxa. Whereas in the intertidal such
427 interventions serve to retain moisture, in the subtidal they may be more important in
428 providing refuge from large-bodied predators, such as fish, which can exert considerable top-
429 down control on the biota on marine infrastructure (Connell & Anderson 1999; Clynick,
430 Chapman & Underwood 2007; Ferrario *et al.* 2016). Depressions can also serve as protection
431 from high wave exposure that can challenge the attachment strength of organisms and

432 interfere with feeding behaviour (Moschella *et al.* 2005; Bulleri & Chapman 2010). In
433 contrast, the elevated structures formed by seeding marine infrastructure with large-bodied
434 habitat-forming taxa or soft structures (e.g. rope) had greater positive influence on subtidal
435 fish than depressions. Such larger-bodied taxa may not fit within the bounds of depressions,
436 and instead, elevated structures may provide shelter and food resources for these (Hair & Bell
437 1992; Fernández *et al.* 2009). However, in the subtidal, a relationship between the body-size
438 of organisms and the dimensions of the interventions that produced the most positive effect
439 sizes was not demonstrated (Fig. 6).

440

441 Although most of the eco-engineering interventions that we reviewed manipulated
442 microhabitats through the addition and/or subtraction of abiotic habitat, approaches that add
443 biotic microhabitat through seeding with habitat-forming species may serve to provide
444 additional benefits (Dafforn *et al.* 2015). Not only may such interventions add habitat, and
445 mitigate the effect of abiotic and biotic stressors on associated organisms (Dafforn, Glasby &
446 Johnston 2012), but they may also play an important role in carbon sequestration (e.g.
447 macroalgae), nutrient cycling and/or maintain clean waters (e.g. filter feeders). Nevertheless,
448 the establishment of habitat-forming taxa remains a challenge on some urban infrastructure
449 (Bulleri & Chapman 2010). For example, while transplant of the canopy-forming algae
450 *Cystoseira barbata* onto breakwaters is technically feasible, survivorship can be limited by
451 grazing, which is more intense than on natural rocky reefs (Perkol-Finkel *et al.* 2012; Ferrario
452 *et al.* 2016). Additionally, because the location of infrastructure is often in areas that suffer
453 from high pollutant loadings and poor water quality, environmental conditions may limit the
454 growth and survivorship of habitat-forming species (Falace, Zanelli & Bressan 2006; Ng *et*
455 *al.* 2015).

456

457 Although our meta-analysis demonstrated predominantly positive effects of microhabitat
458 interventions on the abundance and number of species of key functional groups of organisms,
459 very few of the studies identified and analysed, provided assessment of the proportion of
460 species that were native, non-native or cryptogenic (of unknown origin; e.g. Dafforn, Glasby
461 & Johnston 2012; Sella & Perkol-Finkel 2015). In highly urbanised environments, with a
462 long history of shipping and exploitation, the high proportion of species that are cryptogenic
463 can complicate such assessments (Bishop & Hutchings 2011). Nevertheless, despite such
464 difficulties, a large body of literature suggests that subtidal urban infrastructures support
465 more non-native species than nearby rocky reefs (Dafforn, Glasby & Johnston 2012; Airoidi

466 *et al.* 2015) and sedimentary habitats (Heery *et al.* 2017). Assessing the extent to which
467 native, non-native and cryptogenic species benefit from interventions would help to identify
468 maladaptive scenarios which lead to proliferation of unwanted pest species, as well as
469 approaches that limit such risk. For example, interventions that manipulate microhabitat
470 through the addition of biotic (i.e. habitat-forming species) as opposed to abiotic structure,
471 may lessen risk of rapidly colonising pest species from dominating structures, by pre-empting
472 space that they may otherwise occupy (Dafforn, Glasby & Johnston 2012).

473

474 Our analysis revealed that the majority of eco-engineering interventions involved patch-scale,
475 short-term manipulations of individual microhabitat types. These small-scale interventions do
476 not recreate the properties of contiguous natural habitats, due to their comparatively large
477 edge to interior ratios and small areas (Bender, Contreras & Fahrig 1998). Interventions at the
478 scale of the entire structure remain rare, and consequently, our knowledge of how
479 biodiversity benefits relate to the scale of the infrastructure remains poor. As some mobile
480 species, such as grazers or fish, might require a minimum habitat area in order to effectively
481 forage (Perkins *et al.* 2015), it is expected that a positive relationship between the area of
482 interventions and their effect on biodiversity might emerge as larger-scale interventions are
483 attempted. Additionally, because the majority of monitoring associated with such
484 interventions was also at the patch scale, and rarely extended beyond 12 months (but see
485 Ferse *et al.* 2013) our understanding whether such eco-engineering approaches have
486 biodiversity benefits that extend beyond the site of the intervention or over longer timeframes
487 remains largely unknown. None of the studies tested the benefits of providing habitat
488 complexity at multiple scales.

489

490 The studies assessing the efficacy of eco-engineering interventions came primarily from
491 developed countries in North America, Europe and Australasia. Although this may be a
492 function of both the distribution of coastal ecologists monitoring eco-engineering
493 interventions, and the distribution of eco-engineering interventions themselves, we suspect
494 that the latter is the key driver of this non-random distribution. In terrestrial environments,
495 socioeconomic status is a key indicator of the uptake of eco-engineering interventions such as
496 green walls and roofs, which correlates with factors such as level of education, willingness to
497 pay for environmental improvements, and the resources available for creating an ecological
498 ideal (Kinzig *et al.* 2005; Francis & Lorimer 2011). While such studies are not yet available
499 for the marine environment, we expect similar drivers for the uptake of marine eco-

500 engineering. Quantification of the economic benefits of marine eco-engineering interventions
501 relative to any additional costs associated with their incorporation into structures would help
502 to increase the support for broader-scale implementation.

503

504 While the eco-engineering of marine urban infrastructure has made significant advances in
505 the past few decades, there has been little consideration of how specific local scale abiotic
506 factors (e.g. pollution, temperature, wave exposure) or biotic interactions (e.g. predation,
507 competition, facilitation) influence species interactions and distributions (Bulleri & Chapman
508 2010). This is despite predictions of ecological theory that positive interactions will
509 strengthen across gradients of biotic (e.g., competition, predation, facilitation) and/or abiotic
510 (e.g., temperature, desiccation) stress, while negative interactions will weaken (Bertness &
511 Callaway 1994). Although our review clearly shows that the effects of complex microhabitats
512 are generally positive, the differing effect size of many of the interventions between intertidal
513 and subtidal zones, and between groups of species, highlights the important role that
514 interactions with the environment can play in determining the outcome of eco-engineering.

515

516 The goals of eco-engineering may range from enhancement of biodiversity, to enhancement
517 of specific ecosystem services, such as fisheries productivity, carbon sequestration,
518 maintenance of water clarity and/or nutrient cycling (Chapman & Underwood 2011). The
519 results of this meta-analysis will assist managers and stakeholders in identifying solutions
520 that best match their specific goals. As different groups of organisms responded most
521 strongly to different types of intervention, eco-engineering projects aimed at maximising
522 biodiversity might benefit from the creation of a variety of different types of microhabitats
523 on any given structure, that increase the breadth of niche space available to organisms
524 (Connor & McCoy 1979). In contrast, projects aimed at enhancing fisheries productivity may
525 wish to target those interventions - the addition of water-retaining features to the intertidal or
526 habitat-forming species or structural mimics to the subtidal – that maximise fish abundance.
527 Nevertheless, studies examining the efficacy of eco-engineering interventions in enhancing
528 ecosystem services are rare, and only one study (Loke & Todd 2016) has tested the effects of
529 utilising mosaics of multiple types of interventions. However, this study did not quantify the
530 benefits of adding a mosaic of interventions vs. individual interventions for enhancing the
531 richness for multiple functional groups or habitat-forming taxa (Loke & Todd 2016). Further
532 research is urgently needed on these topics. Recent advances in computation design software
533 and three-dimensional printing technology now allow for bespoke eco-engineering designs to

534 be cheaply and readily developed for individual sites (Loke *et al.* 2014). Such techniques also
535 offer great potential for re-creating structures/surfaces that are more akin to natural
536 shorelines.

537
538 Although the results of this study indicate that eco-engineering interventions enhance the
539 abundance and richness of ecological communities associated with urban infrastructure, it is
540 unclear to what extent these interventions mitigate the impact of replacing natural with
541 artificial habitat. In addition to local-scale impacts on biodiversity, urban infrastructure can
542 impact ecological processes over larger scales by modifying ecological connectivity (Bishop
543 *et al.* 2017) and through the cumulative effects of multiple developments (Dethier, Toft &
544 Shipman 2016). Given that eco-engineering interventions are unlikely to fully compensate for
545 impacts of urban infrastructure, the feasibility of ‘nature-based’ approaches, which entail
546 restoration, conservation or creation of habitats that provide the desired functions of
547 infrastructure, should first be investigated prior to the decision to build new structures
548 (Sutton-Grier, Wowk & Bamford 2015; Dethier, Toft & Shipman 2016). Where it is not
549 possible to avoid the construction or removal of infrastructure, eco-engineering approaches,
550 which are mindful of site characteristics, the local species pool, and project goals, can assist
551 in minimising the ecological footprint.

552

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559

560 **Authors’ contributions**

561 ES and MB conceived the ideas, designed methodology and led the writing of the manuscript.
562 ES analysed the data. All authors collected the data, contributed critically to the drafts and
563 gave final approval for publication.

564

565 **Data accessibility**

566 A list of data sources used in the study is provided in the Data sources section. Further
567 information is also available in Table S1 in online Supporting Information.

568

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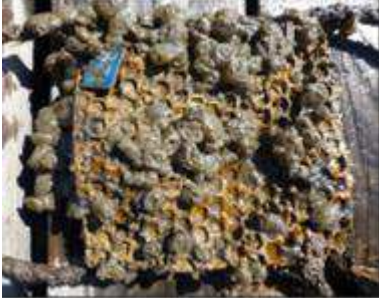



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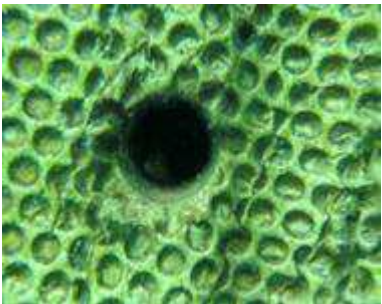



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Table 1: Categories of intervention defined for the meta-analysis and qualitative literature review.

Classification	Description	Image
Texture	micro-scale manipulation applied to an entire intertidal or subtidal surface that produces depressions and/or raises of ≤ 1 mm	
Crevice	intertidal or subtidal depression with a length to width ratio $>3:1$, and depth of >1 mm	
Pit	intertidal or subtidal depressions with a length to width ratio $<3:1$ and depth of >1 mm to 5 cm. This may or may not hold water.	
Intertidal water retaining features	intertidal depressions or features including a) flower pots and b) rockpools with a length to width ratio $<3:1$ that hold water (≥ 5 cm depth) when the tide retreats	<p>a) flowerpot</p>  <p>b) rockpools</p>

		
Subtidal holes	subtidal depressions with a length to width ratio $<3:1$ and ≥ 5 cm depth	
Small elevations	intertidal or subtidal protruding structures (i.e. raises, ledges or ridges) ≥ 1 mm high and < 0.5 m high in dimension	
Large elevations	intertidal or subtidal protruding structures (i.e. raises, ledges, ridges) > 0.5 m high in dimension	
Soft structures	subtidal flexible, protruding materials such as rope, ribbon or twine (>0.1 m in length)	
Habitat-forming	taxa that provide structural habitat to	


taxa	associated organisms (i.e. barnacles, bivalves, coral, canopy-forming algae, branching coralline algae)	
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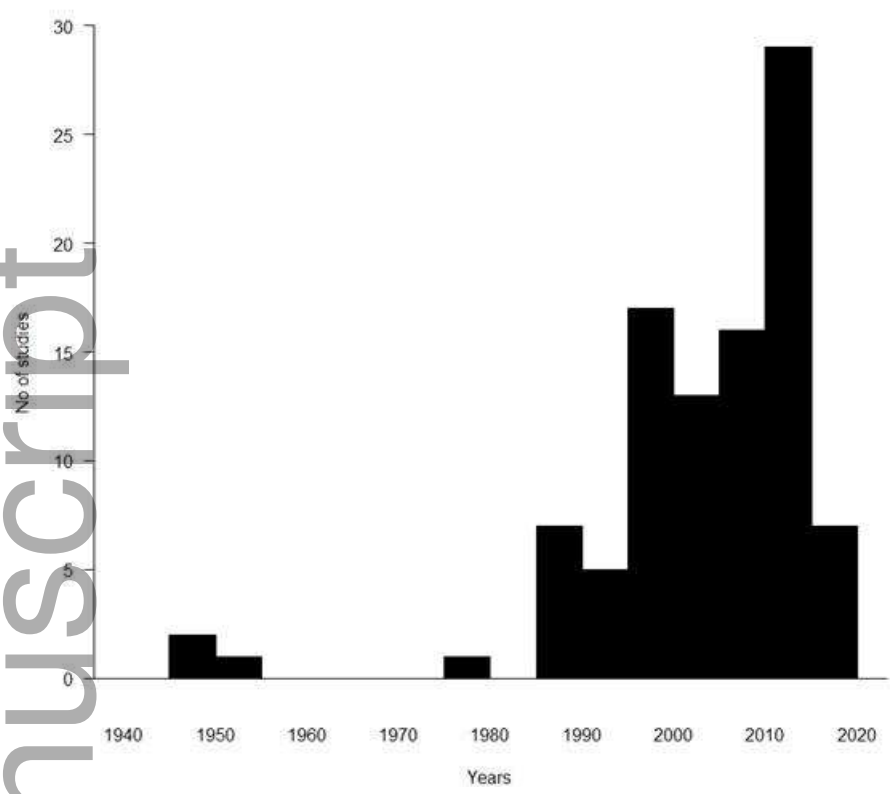
Table 2: Outcome of meta-analyses and qualitative (underlined and in brackets) review. For each intervention we highlight the results of the meta-analysis where available and the results from the qualitative review where there was insufficient information presented to undertake the meta-analysis (see figures for full results). Interventions are scored according to whether they had significant positive (+), negative (-) or non-significant (ns) effects (at $\alpha = 0.05$) relative to controls.

Response	Number of species				Abundance of species				Number of species or abundance of habitat-forming taxa				
Microhabitat	Sessile	Mobile	Benthic	Fish	Sessile	Mobile	Benthic	Fish	Barnacles	Bivalves	Branching coralline	Canopy algae	Coral
Intertidal													
Texture	<u>(ns)</u>				+				+	-	+	<u>(ns)</u>	
Crevice	+	ns	ns		+	<u>(+)</u>	ns		+	+		ns	
Pit			+			<u>(+)</u>	ns		+	<u>(+)</u>	<u>(+)</u>	ns	
Small elevation			ns				ns		<u>(+)</u>	ns		<u>(+)</u>	
Water-retaining	+	ns	+	<u>(+)</u>					ns	ns	+	+	
Seeding	+	ns			ns	<u>(ns)</u>				ns			
Subtidal													
Texture	<u>(ns)</u>				+				-	+	+		<u>(ns)</u>

Crevice	ns				ns				ns	ns		ns	
Pit									<u>(ns)</u>				+
Hole				ns		+		ns					
Large elevation				ns				+					
Seeding	ns			+	ns	ns		ns		ns	ns	ns	ns
Soft structure				+				+					

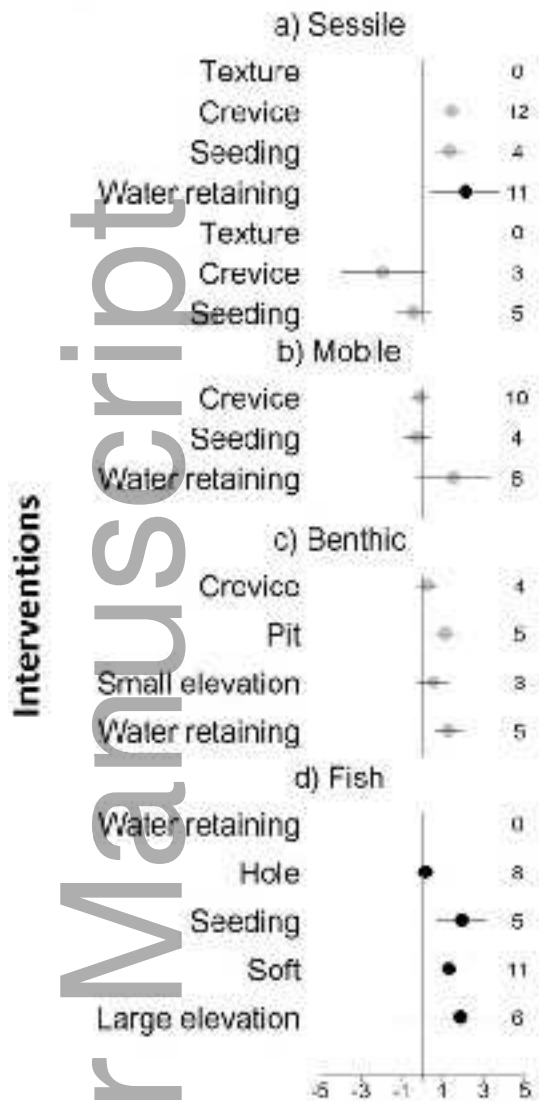


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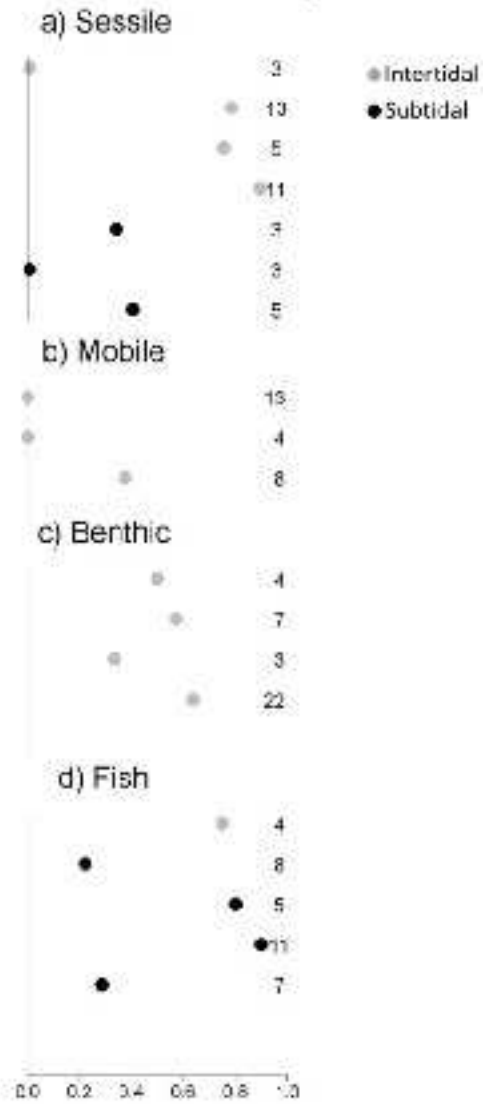


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i) Meta-analysis



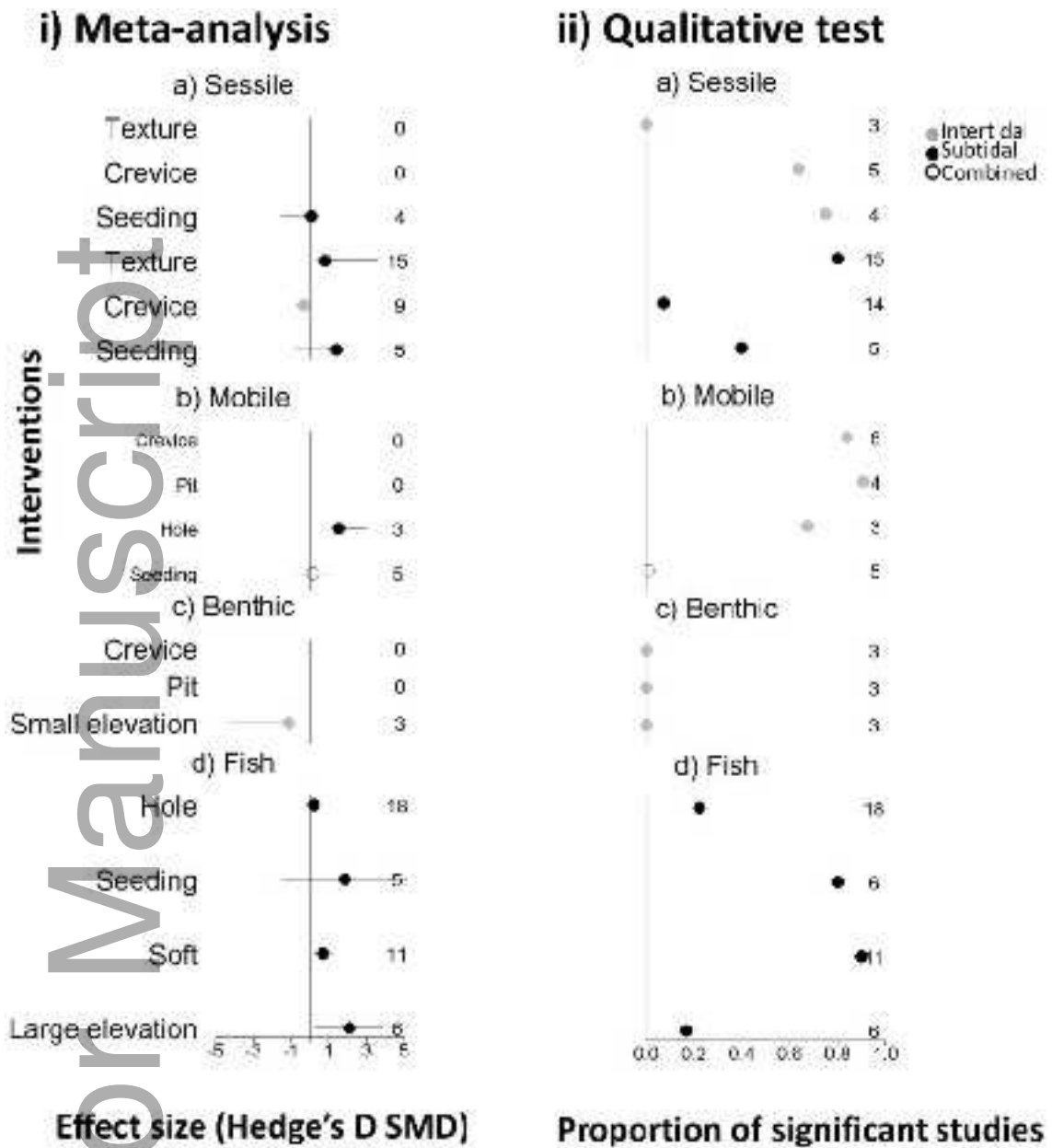
ii) Qualitative analysis



Effect size (Hedge's D SMD)

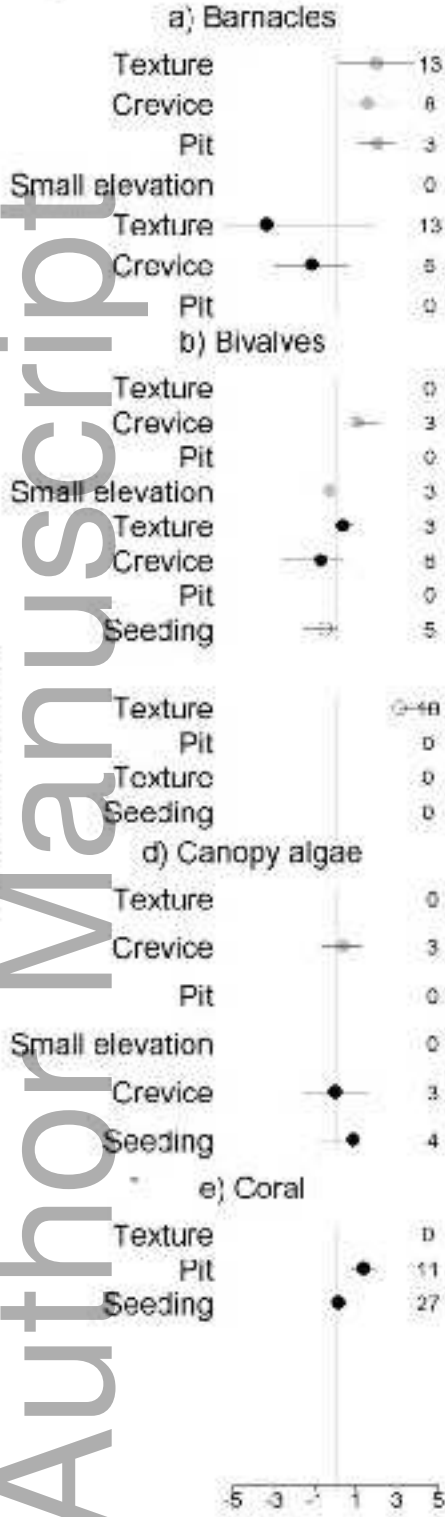
Proportion of significant studies

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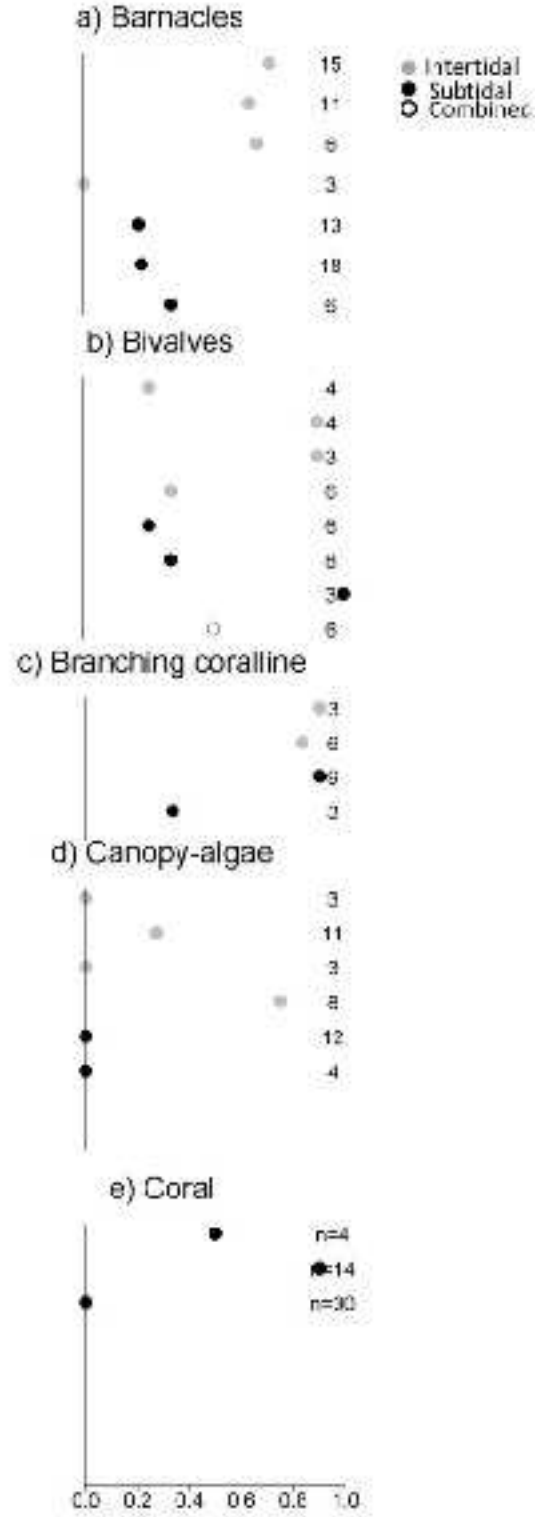


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i) Meta-analysis

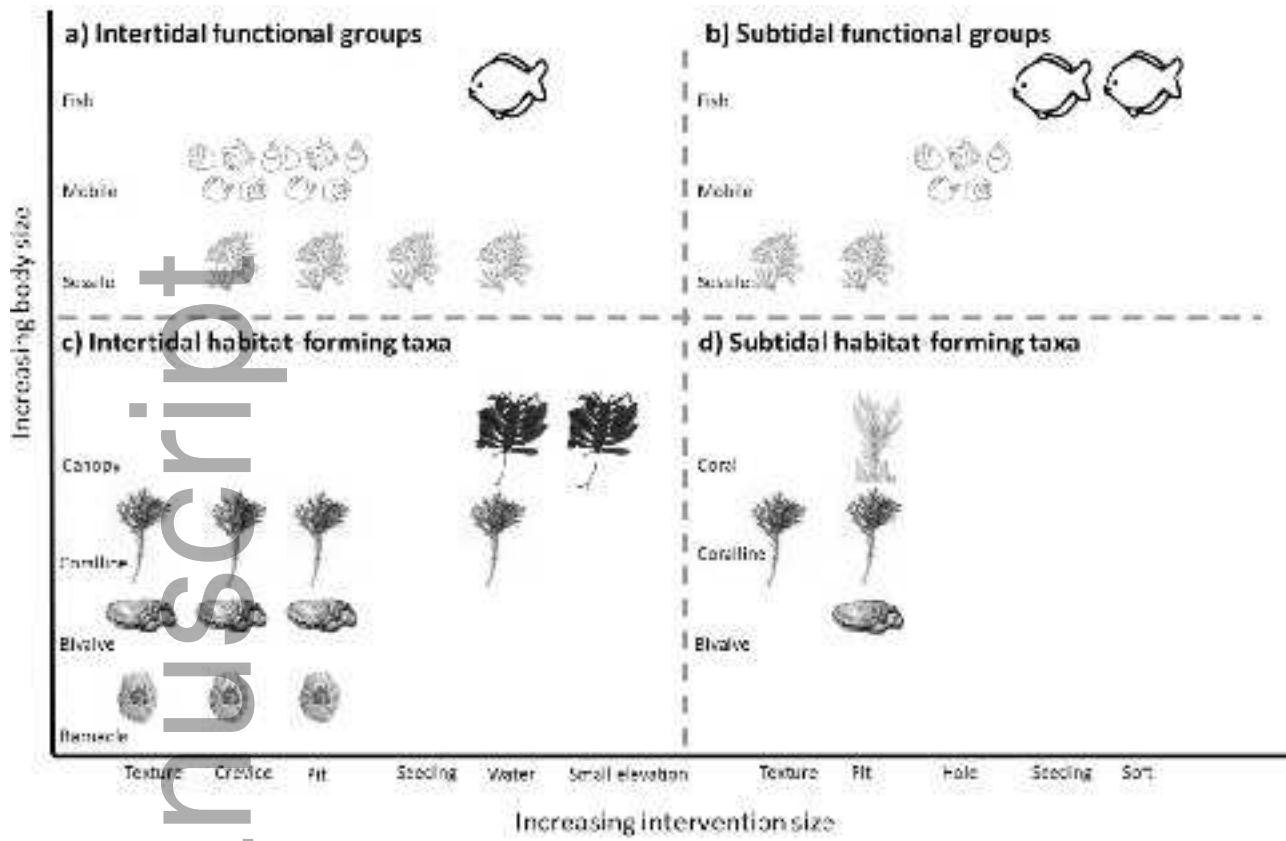


ii) Qualitative test



Effect size (Hedge's D SMD) Proportion of significant studies

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